



## Research Article

## Gradient limits and safety factor of Alpine ibex (*Capra ibex*) locomotion

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### Abstract

Dam walls are like open laboratories useful to study the gradient limits of locomotion. Two dam walls, where Alpine ibex (*Capra ibex*) use to climb searching for the salty exuded, were filmed at 0.2 fps. The straight slope of the walls ranged from 123% to almost vertical. In total 54 animals were filmed and their body mass estimated as medium size, small size and kids. No large males were observed moving on the walls. The overall weighted average incline of their paths was 37% uphill and 46% downhill. They used to climb on zigzag routes and run down on more linear tracks. The gaits employed by the animals were walk and gallop. The steepest paths travelled by kids were 155% up and 157% down, the maximum height was 49 m, while their maximum estimated speeds were 2.6 ms<sup>-1</sup> uphill and -4.2 ms<sup>-1</sup> downhill. Medium: +143% and -157%; 49 m; +1.1 and -4.1 ms<sup>-1</sup>. Large: +102% and -123%; 32 m; +0.7 and -1.0 ms<sup>-1</sup>. The climbing performance of Alpine ibex, in term of speed and inclination, appeared to be negatively influenced by body mass, while the friction coefficient between their hooves and the dam walls was in a range higher than rubber on concrete surfaces. Protection against toppling depends on the slope and the ratio between the basal width and body centre of mass (bCOM) height. We propose a safety factor index (*Fst*), similar to that used in geology, defined as the ratio between the major distance from a downstream to an upstream leg and the centre of mass height, all divided by the tangent of the slope. An index value of “1” is the discriminant between unsafe and relative safe positions. Animals with shorter legs and lower bCOM, like females and kids, can negotiate steeper paths with a higher safety factor.

## Introduction

Many wild plant-eating species can be observed spending time at natural or artificial salt licks, basically to integrate a low-sodium diet (Hebert and Cowan, 1971; Klaus and Schmid, 1998; Ayotte et al., 2006). External dam walls, where salty minerals regularly exude from the concrete bricks, represent a particular kind of salt lick.

Different mountain species, such as the Chamois (*Rupicapra rupicapra*), the Alpine ibex (*Capra ibex*) and even the Alpine marmot (*Marmota marmota*), can be observed climbing several dam walls across the Alps (pers. obs.). However, only the ungulates can reach considerable heights and slopes and Alpine ibex, in particular, are well adapted to move on steep slopes (Geist, 1987). Alpine ibex can most likely be observed on dam walls from late spring to early autumn, when their spatial behaviour is primarily driven by resource exploitation (Scillitani et al., 2012).

Both the cost of walking and running in human increase dramatically with gradient. The same happens, on lower extent, in case of steep negative gradient (Minetti et al., 1993, 2002). Indeed, in such a demanding environment, a strategy to reduce the energy expenditure of locomotion can be crucial (Minetti, 1995). However, Alpine ibex, as other large herbivores, spend the larger part of their time while foraging (Aublet et al., 2009), an activity where the animals are stationary or moving at very low speed (e.g. Brivio et al., 2014). Therefore, beside the high cost of locomotion, alpine ungulates need to deal with the problems, and the related energetic costs, of maintaining a stable position on steep gradient.

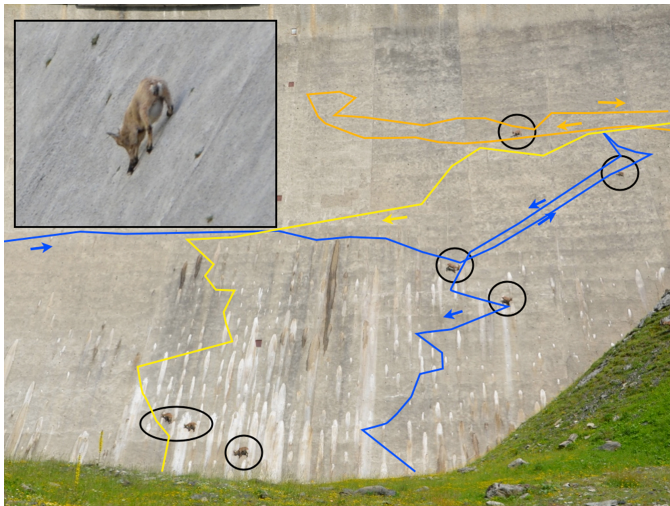
The position of a standing four-legged animal is considered statically stable when the vertical projection of its body centre of mass (bCOM) lies within the boundary of its support pattern, being the support pattern the convex polygon, in a horizontal plane, which contains the vertical projection of all the supporting feet (McGhee and Iswandhi, 1979). However, there can be positions more or less statically stable, and a measure of the magnitude of the static stability, the *Stability Margin*, has been defined as the shortest distance from the vertical projection of the bCOM to any point on the perimeter of the support pattern (McGhee and Frank, 1968).

Several other stability criteria have been proposed for animals or legged vehicles walking on slope or irregular terrains (Hirose et al., 2001). The *Tumble Stability Margin* (Yoneda and Hirose, 1996) evaluates the moment ratio necessary to avoid the tumble around the line connecting two support feet. The *Gradient Stability Margin* and the similar *Tipover Stability Margin* concern the inclination at which a body starts to tumble owing to gravity (Hirose et al., 2001).

In a quadruped animal standing on level, the area of the support pattern (the projection of the support feet onto the horizontal plane) is delimited by a perimeter that coincides with the support boundary (the convex polygon which connect the tips of the support feet). However, when the same animal is standing on slope or rough terrains, the two polygons do not overlap, and could be quite different (Messuri and Klein, 1985). The same authors defined the energy stability level and the *Energy Stability Margin* (ESM; Messuri and Klein, 1985). The former can be calculated for any edge of the support boundary, and is the work required to rotate the body to a position where the vertical projection of the bCOM lies along the edge in question. The ESM is defined as the minimum of the energy stability levels associated with a

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**Figure 1** – Wall of the dam of Piano Barbellino. Superimposed: the reconstructed paths of single animals. In box: the posture of an Alpine ibex on the wall.

support boundary. A stability criterion based on energy is considered the most applicable in practical experiments, but a normalised form has been proposed to avoid the influence of weight on its absolute value (Hirose et al., 2001). In order to achieve an optimally stable position, the bCOM should be located in a position that corresponds to the maximum ESM (Messuri and Klein, 1985). While on slope, the maximum ESM is obtained when the position of the bCOM is shifted towards the uphill direction (Messuri and Klein, 1985).

The patterns of displacement of Alpine ibex on steep slopes, and the relationship between their static and dynamic stability can be of wide interest. Particularly in the field of the biomechanics of animal locomotion, but also for the biological and biomedical disciplines related to the ecology and the management of the species. The current Alpine ibex populations are the result of huge plans of protection and reintroduction (Stüwe and Nievergelt, 1991), and deep knowledge of all the aspects of the biology of the species are crucial for improving their management.

One of the purposes of this work is to investigate about the gradient limit of locomotion in these quadrupeds and, besides, we would like to address the question of the stability of the locomotion on gradient. Our hypotheses are that i) there are gradient limits beyond which standing and moving become unstable; ii) those limits depend on the dimensions and posture of the animals and iii) with respect to other similar sized ungulates, the Alpine ibex presents morphological characteristics that increase their stability on slope.

## Material and Methods

### Field work

Five dams are known to be used by ungulates in Italy, two in Piedmont and three in Lombardy (central-western Alps). The dam walls are made of brickwork with cement (4) or concrete blocks (1), are 24 to 64 m high, with slopes variable from 123% to almost vertical ( $\infty\%$ ). The animals were filmed in two of those locations: i) Lago della Rossa (Valli di Lanzo, Turin, Piedmont, 2716 m a.s.l.), brickwork wall, 24 m high, straight slope of 161% from ground to 19 m, then almost vertical. Pictures taken at 15 s time interval (0.07 fps); ii) Piano Barbellino (Val Seriana, Bergamo, Lombardy, 1868 m a.s.l.), concrete wall, 64 m high, straight slope of 123% from ground to 31 m, then 157% for 22 m, and then almost vertical. Pictures were taken at 5 s interval (0.2 fps). Film footage was taken between July and October during the years from 2010 to 2012. In total 54 alpine ibex were filmed, 21 on the Lago della Rossa dam wall and 33 on the Piano Barbellino one. All the animals were categorised as follow: medium size, small size and kids, based on the number of pixels covered by the silhouette of the animal. No large males were observed climbing the dam walls, while the medium and small sized were either females or young males.

### Assumptions and analyses

The footage were analysed frame by frame. The area captured by the picture was calibrated against two known distances. The error due to linear perspective from the position of the camera was up to a maximum of 6.5%. However, it had minor effect on the ratios used to calculate slopes, speeds and aspect ratios.

The actual slope of the paths followed by the animals was calculated applying common trigonometric formulae to measured variables and constants (Fig. 1, 2, see captions for explanation).

The static and dynamic coefficients of friction of bovidae hooves (*Bos* sp.) on dry and wet abrasive surfaces, like bricks and cement or concrete walls, are in a range of 0.70-0.88 (Bonser et al., 2003). These values are higher than the frictional coefficient of rubber on concrete, but we can assume that in highly specialized mountain goats, like the alpine ibex, the coefficient can be even higher.

### Safety factor

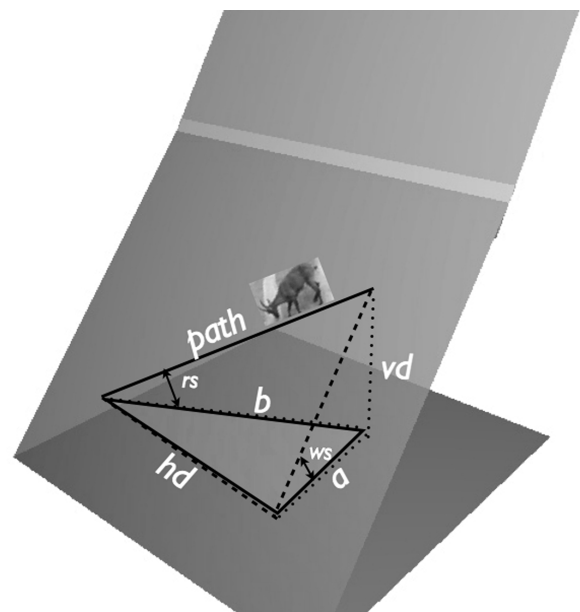
Any solid body resting on an inclined surface is subject to a driving force directed downwards. Such driving force is proportional to the sine of the slope tilt angle ( $\Theta$ ), while the opponent resisting force is proportional to the sine of the friction angle ( $\Phi$ ), defined as the angle of a plane to the horizontal when a body placed on the plane will just start to slide. The tangent of the angle of friction is the coefficient of static friction. When the resisting force is not strong enough to balance the driving force, the body can either slip or topple over. Slip is a sliding movement, while toppling involves a rotation of the body. These two movements have been modelled and analysed in geoscience, in order to evaluate the behaviour of rocks resting on inclined surfaces (West, 1995; Haneberg, 2009).

The variables in the running are the mentioned angles ( $\Theta$  and  $\Phi$ ), the breadth, in the direction of the slope ( $b$ ), and the height of the resting body ( $h$ ). The scenario considers four combinations:

- $\Theta < \Phi$  and  $b/h > \tan\Theta$ : stable, no slipping and no toppling
- $\Theta > \Phi$  and  $b/h > \tan\Theta$ : unstable, slipping but no toppling
- $\Theta < \Phi$  and  $b/h < \tan\Theta$ : unstable, toppling but no slipping
- $\Theta > \Phi$  and  $b/h < \tan\Theta$ : unstable, slipping and toppling

The *safety factor* ( $Fst$ ) defined in geology to evaluate the probability of toppling of resting rocks is:

$$Fst = \frac{b}{h} \frac{1}{\tan\Theta}$$



**Figure 2** – Real slope ( $rs$ ) and distance ( $path$ ) computation:  $vd$  = measured vertical displacement (m);  $hd$  = measured horizontal displacement (m);  $ws$  = known wall slope angle (rad);  $a = vd / \tan(ws)$ ;  $b = \sqrt{a^2 + hd^2}$ ;  $\tan(rs) = vd / b$ ;  $path = vd / \sin(rs)$ . From those relationships is clear that the slope, expressed as percentage, is equal to the tangent of the slope angle multiplied by 100 (e.g.:  $\Theta = 52^\circ$  (0.91 rad);  $\tan(\Theta) = 1.23$ ; slope = 123%).



Where the body is considered safe when  $Fst \geq 1$ . Plotting the ratio  $b/h$  against the slope we obtain a plane where the point with the same safety factor lie on hyperbolas.

We propose to adopt a similar concept of safety factor for animals resting or moving on incline. However, while rocks are strictly rigid body, animals can move and, in particular, their bCOM can change position depending on morphological and postural characters. Therefore, differently from geologists, we would define  $h$  as the vertical height of the bCOM and  $b$  as the major distance between a downstream and an upstream support leg (Fig. 3). To test our third hypothesis, we estimated the  $b/h$  ratio of ibex (males, females and kids) and of two other artiodactyl species for comparison. We chose the roe deer (*Capreolus capreolus*) and the fallow deer (*Dama dama*) for their size, comparable to the size of alpine ibex, for their habitat, different from that of ibex, and for being not strictly relatives of ibex (distinct family).

Statistical analyses

Statistical differences between slopes of uphill and downhill paths have been assessed using the non-parametric Freidman test (Sokal and Rohlf, 1995). Linear regression analysis have been performed using slopes as independent variable and speed as dependent (Sokal and Rohlf, 1995). Analyses have been performed using the software pack-age SPSS (v20, IBM).

Results

Gradients

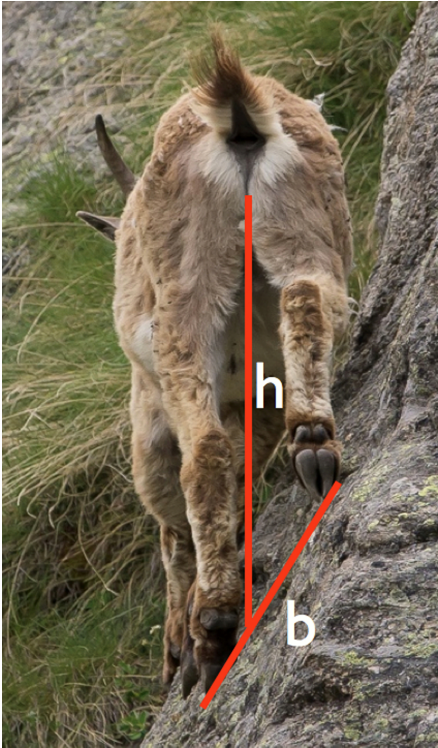
The calculated total linear distance of the monitored paths was 1870 m, covered by the animals at an average speed of  $0.6\text{ ms}^{-1}$  ( $2.2\text{ kmh}^{-1}$ ). The overall weighted average incline of their paths was 37% (median 34%) uphill and 46% (median 38%) downhill (Fig. 4). They used to climb on zigzag routes and run down on more linear tracks, with a slight tendency to follow steeper downhill paths, but the differences were not statistically significant (Friedman 2-way ANOVA by ranks,  $p=0.292$ ). The modal rank during uphill locomotion was +31 to +40% (179 m of paths covered), while only 8 m were covered at gradients steeper than +100%. In downhill locomotion the modal rank was -11 to -20% (180 m), while 143 m were covered in the average rank (-41 to -50%), and 80 m at gradient steeper than -100%. The steepest paths travelled by kids were 155% up and 157% down, the maximum height on the wall was 49 m, while their maximum estimated speeds were  $2.6\text{ ms}^{-1}$  uphill and  $-4.2\text{ ms}^{-1}$  downhill. Small size ibex: +143% and -157%; 49 m; +1.1 and  $-4.1\text{ ms}^{-1}$ . Medium size: +102% and -123%; 32 m; +0.7 and  $-1.0\text{ ms}^{-1}$ . Larger and heavier animals showed a tendency to move slowly than light ones (Fig. 5).

Gaits and speed

The usual gait employed by animals was walking and gallop. While licking exuded salt, adult alpine ibex could move uphill sideway, employing the adaptive intermittent crawl pattern described by Konno et al. (2003). When moving at higher speed, they usually employed gallop rather than trot. The speed decreased nearly with the cubic root of the slope, in both directions. The exponents of the linear regression of log-transformed speed (dependent) versus slope (independent) were -0.30 uphill ( $p<0.001$ ) and -0.37 downhill ( $p<0.001$ ).

**Table 1** – Safety factor for *Capra ibex*. Class: the 4 size categories defined. Light size were only females, Medium size were both heavier females and young males, Heavy were the big males (never observed climbing the walls);  $b/h$ : the ratio as defined in the text;  $Fst(1)$ : the safety factor at 123% gradient (50.8°);  $Fst(2)$ : the safety factor at 157% gradient (57.5°). In **bold** the animal actually observed at that gradient.

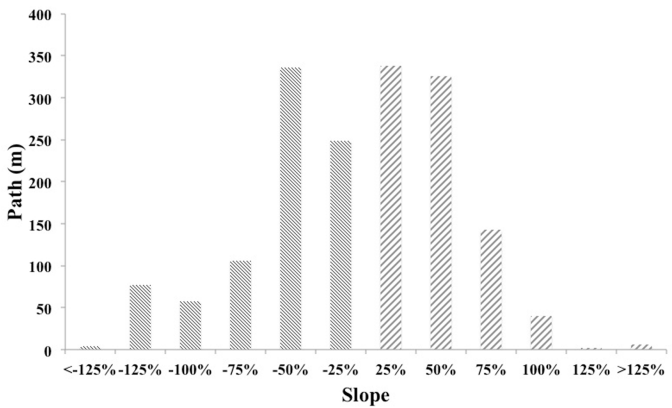
Class	$b/h$	$Fst(1)$	$Fst(2)$
Kid	1.99	<b>1.62</b>	<b>1.27</b>
Light F	1.43	1.17	<b>0.91</b>
Medium F/M	1.23	<b>1.00</b>	0.78
Heavy M	0.87	0.71	0.55



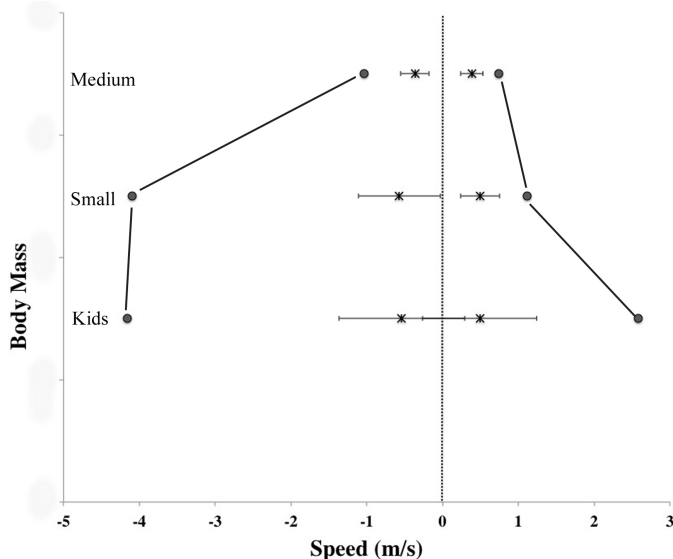
**Figure 3** – Alpine ibex on a natural steep slope (Photo by A. Balestra).  $b$  is the major distance between the most downstream and the most upstream foot;  $h$  is the height of the centre of mass.

Safety factor

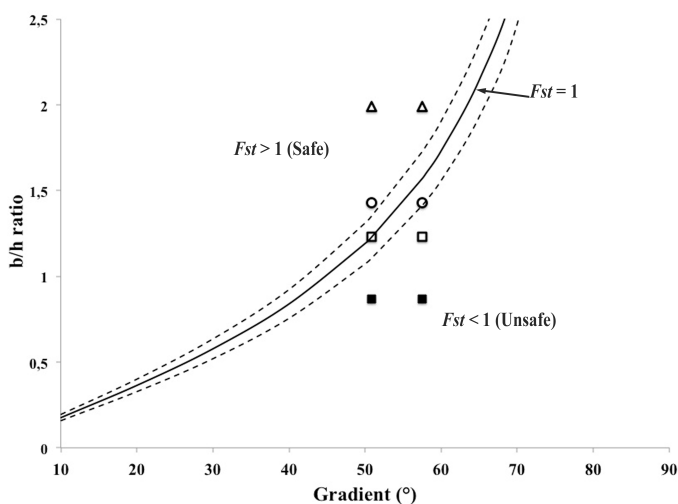
It has not been possible to take the real measures of the animals observed moving on the dam walls, but only classify them into dimension categories. Therefore, in order to test our hypothesis, we made some assumptions: i) to make a first computation we considered the distance  $b$  as fixed value, independent from sex, age and dimension. Further we assumed the pelvis width (distance between the two femur heads), measured in a previous work (Biancardi and Minetti, 2012), as a proxy for such a distance; ii) we considered the height at the whitters of adult males and females reported by Tosi and Pedrotti (2003) as a proxy for the vertical height of the bCOM; iii) we corrected the heights of females by multiplying them for 0.9, to compensate the different mass of the horns (lighter in females in the order of tens); iv) we computed the height of kids as 2/3 of the height of females, based on an average comparison (pixel count) of HD images of kids and females; v) in order to get more manageable numbers in the ratio  $b/h$ , we intentionally took the measures of  $b$  in millimetres and that of  $h$  in centimetres (we return on this in the discussion).



**Figure 4** – Calculated paths per positive (uphill) and negative (downhill) gradient.



**Figure 5** – Speed per body class and gradient (uphill and downhill). Average  $\pm$  SD and maximum values..



**Figure 6** – Safety factor per gradient (in abscissa). On ordinate the b/h ratio. The curved line joins the points with  $Fst = 1$  ( $\pm 5\%$ , dashed lines). Open triangles = kids; open circles = small females; open squares = middle females and young males; filled squares = large males.

In Tab. 1 the results, plotted in graph (Fig. 6). Kids, females and young males showed a  $Fst \geq 1$  at a gradient of 123%, while at the steeper gradient only kids and light females were in the “safe” zone. For comparison, we computed the  $Fst$ , at the gradient of 123%, for adult roe deer and for males and females of the fallow deer, using the data collected from our previous work (Biancardi and Minetti, 2012). In all cases the estimated  $Fst$  resulted  $< 1$ .

## Discussion

The purpose of this research was to investigate the gradient limits of locomotion of a specialised mountain ungulate, the alpine ibex, in a particular context represented by dam walls used as salt licks. As pointed out by Niederberger (1993), salt licks are used mainly (but not exclusively) by females, kids and young ibex. We argue that, in the case of dam walls, physical reasons relating to the hazards of moving on such steep slopes are involved as well.

The locomotion on gradient has been widely studied in humans (Minetti, 1995; Minetti et al., 2002). The mechanical external work, equally divided into positive and negative work on level, become totally positive or totally negative at gradient of +15% and -15% respectively (Minetti et al., 1993). Accordingly, the cost of locomotion rapidly

increase with positive gradients, while on negative ones it firstly decreases, but shortly it starts to grow again (Saibene and Minetti, 2003).

The vertical cost of walking and running ( $J kg^{-1} mvert^{-1}$ ) is defined as the energy expenditure to walk or to run a distance that corresponds to a vertical displacement of 1 m. In humans the vertical cost of uphill walking presents a minimum value of  $45 J kg^{-1} m^{-1}$  in the slope range of 20-40% (Minetti et al., 2002). The only data available for mountain goats (*Oreamnos americanus*) and bighorn sheep (*Ovis canadensis*), came from Dailey and Hobbs (1989), which reported a vertical cost of locomotion of  $37 J kg^{-1} m^{-1}$  on a positive gradient of 39%. On the other hand, Fancy and White (1987) reported a vertical cost of  $23 J kg^{-1} m^{-1}$  at a gradient of +11%, in caribous (*Rangifer tarandus granti*). Different paths could be chosen to overcome a height difference: longer and easier or shorter and steeper. The optimal path follow a gradient that minimize the vertical cost of locomotion (Minetti, 1995).

It is likely that an optimum gradient exists for ibex, and goats in general, as well. Based on the number of meters traveled at different ranks of gradients, the preferred or optimum could be in the range 30-40%. In downhill locomotion the cost is much less, due to the eccentric muscular work that is needed to dissipate the negative work. With respect to positive gradient, steeper and longer paths were traveled downhill. The velocities are very low, and therefore the animals, even during the steeper transitions, were not likely to present problems of metabolic power.

Gallop was preferred to trot for its greater stability, being an asymmetric gait (Biancardi and Minetti, 2012), like skipping (Minetti et al., 2012; Pavei et al., 2015). Adaptive dynamic walking has been widely investigated, in order to build legged robot moving on irregular terrains (Kimura et al., 2001; Fukuoka et al., 2003; Kimura et al., 2007). However, those models, which used a CPG (central pattern generator) cycle based control, were difficult to adapt to a steep slope (Aoyama et al., 2008).

In order to maintain quite constant the stability margin, an adaptive intermittent crawl gait has been described for quadruped walking robot (Konno et al., 2003). However, with such crawl gait, the high stability is obtained at the expense of speed. An optimal body posture with the maximum possible moving speed on slope has been modelled by Zhang et al. (2005) and Zhang and Inoue (2006), and experienced in different experiments with quadruped robots (Hirose et al., 1997; Hodoshima et al., 2004; Doi et al., 2005).

One of the problems faced by quadrupeds walking on slope is maintaining an optimal joint torque. Aoyama et al. (2008) approached the question with both numerical simulation and experiments with robots, finding that smaller rates of rear leg length (i.e. forelegs longer than hind legs) gave an advantage in terms of cost function of torque.

The safety factor ( $Fst$ ) that we propose differs from the one employed in geology (West, 1995). The main differences are related with the measure of the height, as explained in materials and methods, and in the



**Figure 7** – Change of posture on quasi-vertical slope. Left: Lago della Rossa dam (Photo by L. Ciaudano); Right: Cingino dam (Photo by G. Gruttadauria).



calculation of the ratio  $b/h$ , as explained in results. Taking the measure of  $b$  in mm and that of  $h$  in cm practically means to amplify the base (b) and raise the ratio by a factor of ten. As a result, an animal would have almost the same safety factor of a tenfold lower rock.

This is indeed a huge change. However, we should consider that a rock lies passively on the terrain, exerting a constant force due to gravity, while an animal would continuously exerts differential forces through their limbs, due to muscular work for postural arrangements. Those postural arrangements typically increase the stability, and then could be, in our opinion, a reliable factor of such increase.

One bias that occurred in the estimated values obtained was due to the fixed value of  $b$ . This parameter represents the distance, in the direction of the slope, between the most uphill and the most downhill support (foot). Taking  $b$  as a fixed value introduced two errors: i) an error due to the different size of the animals, which could bring to an overestimation of the  $Fst$  for smaller individuals, namely the kids; ii) an error due to both, the possibility for an animal to modify the distance changing the position of the feet, and the fact that the linear distance between two feet on gradient (hypotenuse) is larger than their horizontal linear distance (cathetus). The latter could bring to a general underestimation of  $Fst$ .

Considering the assumptions and the biases, we however think that our results represent a good approximation, and that they can give a good idea of what is going on for animals moving on a steep slope.

Comparing the results with the observations and the data collected by photo and video recording, we can take the following conclusions: i) ibex with an estimated  $Fst < 1$  at the minor gradient (123%), i.e. the adult males, never went on the dam wall; ii) ibex with an estimated  $Fst \approx 1$  at the minor gradient, i.e. some females and young males, were not likely moving to the steeper gradient; iii) when moving at  $Fst \approx 1$  or less, the ibex are likely to adopt postural changes in order to enlarge the length of the support base ( $b$ ), and therefore  $Fst$ ; iv) in order to reach very steep part of the wall, as in the case of Lago della Rossa dam, ibex adopt a quasi-bipedal posture (Fig. 7), with the hind feet downhill and the forefeet uphill, in order to have the maximum length of the support base ( $b$ ).

The definition of a safety factor, aside from discriminate among permitted, hazardous and not-permitted posture and slopes combinations, can be useful to investigate among adaptations to mountain environments in different species. Standing positions and movements at slow speeds are of great importance for several aspects of mammal life, such as foraging, mating and others (e.g.: Brivio et al., 2014). Therefore knowing the physiological limits of locomotion in such demanding environment can improve the knowledge of ecological and ethological aspects as well. Finally, the detection of unexpected salt lick sites, and the evaluation of species or classes of individuals that can potentially benefit of them, can be of aid in the management of alpine species. ☞

## References

Aoyama T., Sekiyama K., Hasegawa Y., Fukuda T., 2008. Analysis of Relationship between limb length and joint load in quadruped walking on the slope. *Intelligent Robots and Systems*, 2008. IROS 2008. IEEE/RSJ International Conference, pp. 3908–3913.  
 Aublet J.F., Festa-Bianchet M., Bergero D., Bassano B., 2009. Temperature constraints on foraging behaviour of male Alpine ibex (*Capra ibex*) in summer. *Oecologia* 159(1): 237–247.  
 Ayotte J., Parker K., Arocena J., Gillingham M., 2006. Chemical composition of lick soils: Functions of soil ingestion by four ungulate species. *J. Mammal.* 87: 878–888.  
 Biancardi C.M., Minetti A.E., 2012. Biomechanical determinants of transverse and rotary gallop in cursorial mammals. *J. Exp. Biol.* 215: 4144–4156.  
 Bonser R.H.C., Farrent J.W., Taylor A.M., 2003. Assessing the frictional and abrasion-resisting properties of hooves and claws. *Biosystems engineering*. 86(2): 253–256.

Brivio F., Grignolio S., Brambilla A., Apollonio M., 2014. Intra-sexual variability in feeding behaviour of a mountain ungulate: size matters. *Behavioral Ecology and Sociobiology* 68(10): 1649–1660.  
 Dailey T.V., Hobbs N.T., 1989. Travel in alpine terrain: energy expenditures for locomotion by mountain goats and bighorn sheep. *Can. J. Zool.* 67: 2368–2375.  
 Doi T., Hodoshima R., Hirose S., Fukuda Y., Okamoto T., Mori J., 2005. Development of a quadruped walking robot to work on steep slopes, TITAN XI (walking motion with compensation for compliance). *Intelligent Robots and Systems*, 2005. (IROS 2005). 2005 IEEE/RSJ International Conference, pp. 2067–2072.  
 Fancy S.G., White R.G., 1987. Energy expenditures for locomotion by barren-ground caribou. *Can. J. Zool.* 65: 122–128.  
 Fukuoka Y., Kimura H., Cohen A., 2003. Adaptive dynamic walking of a quadruped robot on irregular terrain based on biological concepts. *Int. J. Robotics Res.* 22: 187–202.  
 Geist V., 1987. On the evolution of the Caprinae. In: *The biology and management of Capricornis and related mountain antelopes*. Proceedings of the International Symposium on Capricornis and its related species. Croom Elm, London.  
 Haneberg W.C., 2009. Simplified Dynamic Analysis of Vibration-Induced Rock Toppling. *Environ. Eng. Geosci.* 15: 41–45.  
 Hebert D., Cowan I.M., 1971. Natural salt licks as a part of the ecology of the mountain goat. *Can. J. Zool.* 49: 605–610.  
 Hirose S., Tsukagoshi H., Yoneda K., 2001. Normalized energy stability margin and its contour of walking vehicles on rough terrain. *Robotics and Automation*, 2001. Proceedings 2001 ICRA. IEEE International Conference, pp. 181–186.  
 Hirose S., Yoneda K., Tsukagoshi H., 1997. TITAN VII: quadruped walking and manipulating robot on a steep slope. *Robotics and Automation*, 1997. Proceedings., 1997 IEEE International Conference, pp. 494–500.  
 Hodoshima R., Doi T., Fukuda Y., Hirose S., Okamoto T., Mori J., 2004. Development of TITAN XI: a quadruped walking robot to work on slopes. *Intelligent Robots and Systems*, 2004. (IROS 2004). Proceedings. 2004 IEEE/RSJ International Conference, pp. 792–797.  
 Kimura H., Fukuoka Y., Cohen A., 2007. Adaptive dynamic walking of a quadruped robot on natural ground based on biological concepts. *Int. J. Robotics Res.* 26: 475–490.  
 Kimura H., Fukuoka Y., Konaga K., 2001. Adaptive dynamic walking of a quadruped robot using a neural system model. *Adv. Robot.* 15: 859–878.  
 Klaus G., Schmid B., 1998. Geophagy at natural licks and mammal ecology: a review. *Mammalia* 62: 482–498.  
 Konno A., Ogasawara K., Hwang Y., Inohira E., Uchiyama M., 2003. An adaptive gait for quadruped robots to walk on a slope. *Intelligent Robots and Systems*, 2003. (IROS 2003). Proceedings. 2003 IEEE/RSJ International Conference, pp. 589–594.  
 McGhee R.B., Frank A.A., 1968. On the stability properties of quadruped creeping gaits. *Mathematical Biosciences* 3: 331–351.  
 McGhee R.B., Iswandhi G.L., 1979. Adaptive Locomotion of a Multilegged Robot over Rough Terrain. *Systems, Man and Cybernetics*, IEEE Transactions 9: 176–182.  
 Messuri D., Klein C.A., 1985. Automatic body regulation for maintaining stability of a legged vehicle during rough-terrain locomotion. *J. Robotics Autom.*, IEEE 1: 132–141.  
 Minetti A., 1995. Optimum gradient of mountain paths. *J. Appl. Physiol.* 79: 1698–703.  
 Minetti A.E., Ardigò L.P., Saibene F., 1993. Mechanical determinants of gradient walking energetics in man. *J. Physiol.* 472: 725–735.  
 Minetti A.E., Moia C., Roi G.S., Susta D., Ferretti G., 2002. Energy cost of walking and running at extreme uphill and downhill slopes. *J. Appl. Physiol.* 93: 1039–46.  
 Minetti A.E., Pavei G., Biancardi C.M., 2012. The energetics and mechanics of level and gradient skipping: preliminary results for a potential gait of choice in low gravity environments. *Planet. Space Sci.* 74: 142–145.  
 Niederberger R.J., 1993. Reaktion der Steinböcke auf künstlich angelegte Salzlecken. *Cratschla* 1:35–39.  
 Pavei G., Biancardi C.M., Minetti A.E., 2015. Skipping vs. running as the bipedal gait of choice in hypogravity. *J. Appl. Physiol.* 119: 93–100.  
 Saibene F., Minetti A.E., 2003. Biomechanical and physiological aspects of legged locomotion in humans. *Eur. J. Appl. Physiol.* 88: 297–316.  
 Scillitani L., Sturaro E., Monaco A., Rossi L., Ramanzin M., 2012. Factors affecting home range size of male Alpine ibex (*Capra ibex ibex*) in the Marmolada massif. *Hystrix* 23(2): 19–27.  
 Sokal R.R., Rohlf F.J., 1995. *Biometry*. New York, NY, WH Freeman & Co.  
 Stüwe M., Nievergelt B., 1991. Recovery of alpine ibex from near extinction: the result of effective protection, captive breeding, and reintroductions. *Applied Animal Behaviour Science* 29(1): 379–387.  
 Tosi G., Pedrotti L., 2003. *Capra ibex* L. In Boitani L., Lovari S., Vigna-Taglianti A. (Eds.). *Fauna d'Italia Mammalia III Carnivora-Artiodactyla*. Calderini, Bologna, pp. 364–434.  
 West T.R., 1995. *Geology Applied to Engineering*. Long Grove, IL, Waveland Press.  
 Yoneda K., Hirose S., 1996. Tumble stability criterion of integrated locomotion and manipulation. *Intelligent Robots and Systems '96, IROS 96*, Proceedings of the 1996 IEEE/RSJ International Conference, pp. 870–876.  
 Zhang L., Ma S., Inoue K., 2006. Several Insights into Omnidirectional Static Walking of a Quadruped Robot on a slope. *Intelligent Robots and Systems*, 2006 IEEE/RSJ International Conference, pp. 5249–5254.  
 Zhang L., Ma S., Inoue K., Honda Y., 2005. Omni-directional Walking of a Quadruped Robot with Optimal Body Postures on a Slope. *Robotics and Automation*, 2005. ICRA 2005. Proceedings of the 2005 IEEE International Conference, pp. 2976–2981.